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PENSOFT

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Discordance between biological and genetic traits highlights complex evolutionary history in the False Apollo, *Archon apollinus* (Herbst, 1798) (Lepidoptera, Papilionidae, Parnassiinae)

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Abstract

The population structure within *Archon apollinus* (Herbst, 1798) across its range has been investigated using mtDNA COI sequences alongside five other gene regions for select samples in order to strengthen the phylogenetic backbone. Results strongly indicated the presence of two highly divergent lineages within this species: One confined to Western Turkey, Northeast Greece as well as the East Aegean islands (*A. apollinus*), and another in central Anatolia and the Levant. Accordingly, we recognize the Levantine lineage as a distinct species, *A. bellargus* Staudinger, [1892], **stat. nov.** Phenotypic differences between adults from western Turkey/Greece and the Levant, partly divergent flight times and significant morphological and ethological differences in caterpillars and pupae support these findings. While our central Anatolian samples were unambiguously part of the Levantine clade (*A. bellargus*), the life history data placed these populations closer to those in western Turkey (*A. apollinus*). The cause and consequences of this discordance are discussed.

Zusammenfassung

Die Populationsstruktur von *Archon apollinus* (Herbst, 1798) wurde in seinem gesamten Verbreitungsgebiet hinsichtlich mtDNA COI und fünf weiterer Genregionen anhand ausgewählter Individuen genetisch untersucht. Die Ergebnisse deuten innerhalb dieser Art stark auf die Existenz von zwei signifikant voneinander abweichenden Linien hin: Eine, beschränkt auf den Westen der Türkei, Nordostgriechenland sowie die griechischen Inseln und eine andere in Zentralanatolien und der Levante. Dementsprechend wird die levantinische Linie als taxonomisch distinkte Spezies eingeordnet - *A. bellargus* Staudinger, [1892], **stat. nov.** Phänotypische Unterschiede zwischen adulten Tieren aus der Westtürkei/Griechenland und der Levante, teilweise abweichende Flugzeiten und signifikante morphologische und ethologische Unterschiede bei Raupen und Puppen bestätigen diesen Befund. Obwohl zentralanatolische Populationen eindeutig dem levantinischen Genotypus angehören (*A. bellargus*), sprechen phaenotypische und ethologische Merkmale für eine Zuordnung zu westtürkischen Populationen. Die Ursachen und Konsequenzen dieser Diskrepanz werden diskutiert.

Key Words

Anatolia, *Aristolochia*, gene tree vs. species tree, Swallowtail butterflies, taxonomic ranking

Introduction

Distributed from northeastern Greece and the east Aegean islands to Turkey, Syria and the Levant, *Archon apollinus* (Herbst, 1798) is one of the most prominent and taxonomically well-studied species in the subfamily Parnassiinae. The great range of regional variability displayed by this species, comparable to those in members of its sister-genus *Parnassius*, has led authors to describe numerous subspecies and forms (Koçak 1982; De Freina 1985).

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Many of these names have now been synonymized, and recent reviews recognize between four and six valid subspecies (Bollino and Racheli 2012; von Stetten and Bozano 2021). The type locality of *A. apollinus* is the Urla Peninsula in Izmir, western Turkey (Herbst, 1798). The majority of the other subspecies are also described from Turkey, including ssp. *amasina* Staudinger, 1901 (TL: "Pont[us]; Kurd[istan]. oc[ccidentalis]"), ssp. *forsteri* Koçak, 1977 (TL: Kastamonu, vicinity of Ödemiş), and ssp. *nikodemusi* Stüning & Wagner, 1989 (TL: "Ambarli/Çekmece, Thrazien"). Two subspecies are described from Syria: ssp. *bellargus* Staudinger, [1892] (TL: "Kessab aus dem südlichen Antiochien") from the far north of Syria close to the border with the Turkish province of Hatay, and ssp. *drusica* de Freina & Leestmans, 2003 (TL: "Djebel ed Druz") from southwestern Syria. Modern reviews classify the Levantine populations from Hatay to Lebanon, Southern Syria and Israel under the subspecific name *A. apollinus bellargus*, with *drusica* as its synonym (von Stetten and Bozano 2021). Morphologically, the adults from the type locality of *bellargus* in Northern Syria and Hatay tend more towards the central Anatolian phenotype, while those further south appear more distinct, suggesting the presence of a clinal gradient.

A deep divergence of COI sequences (2.7%) between Turkish/Greek populations and those in Israel was first reported by Nazari and Sperling (2007) and later confirmed by Condamine et al. (2018). Even though this falls well outside the range of average intra-species variation in Lepidoptera (Hebert et al. 2003), no further research has been conducted on this case of cryptic diversity. A comparative analysis of genetic distances between *A. apollinus* and the other two species in *Archon*, i.e. *A. apollinaris* (Staudinger, [1892]) and *A. bostanchii* de Freina & Naderi, 2003 is also lacking. Here, with extended sampling from many populations across their range, we studied the genetic structure within *A. apollinus* and its congeners, aiming to answer the following questions: 1) are the Levantine and the Turkish/Greek populations of *A. apollinus* specifically distinct? and 2) Are the central Anatolian populations of *A. apollinus* more closely related to those in the Levant or those in western Turkey/Greece?

Materials and methods

Morphology and biology

A total of 260 butterflies from the private collections Prof. Klaus Rose (Mainz) and Dr. Thomas Witt (München) were examined. Dorsal and ventral surfaces of all specimens were photo-documented with a digital high resolution full-frame sensor camera under standardized, shadeless lighting conditions. The specimens were arranged in locality groups and visually compared to assess similarities and differences. A subset of specimens was selected and sampled for DNA sequencing. Genitalia dissections were carried out by MvS using the methodology outlined by Higgins (1975). To compare larval morphology of different populations, field photos of the larvae of *Archon* from Syria: Golan Heights (n = 30), Bet Shemesh (n = 97), southern Turkey: Antakya (n = 123), central Turkey: Ovacic (n = 12) and western Turkey: Alexandria Troas (n = 78) were compared.

Molecular methods

Two legs from dried adult specimens, or dried larval tissue remnants (exuviae) from various populations of *A. apollinus*, as well as *A. apollinaris* and *A. bostanchii* were sampled. Standardized procedures were used to obtain the barcodes at the Center for Biodiversity Genomics in Guelph, Canada. Most samples yielded full-length COI barcode sequences (658 base pairs). Thirteen unpublished COI sequences of various lengths obtained previously by the first author via Macrogen Europe, the Netherlands, were also added to our dataset. Thirty additional COI sequences of *Archon* were retrieved from GenBank and added to the dataset, with two others (EF473830 and KJ020266) excluded due to suspicion of contamination. Sixty-one new sequences were deposited on GenBank (Accessions PV252002–PV252047, PV277995, PV634285–PV634298) (Table 1). Specimen data and images are publicly available in the BOLD dataset "DS-ARCHON" (dx.doi.org/10.5883/DS-ARCHON). Single representatives of the four species in *Luehdorfia*, well-established as the sister genus to *Archon* in the tribe Luehdorfiini (Omoto et al. 2004; Nazari et al. 2007; Nazari and Sperling 2007; Condamine et al. 2018; Allio et al. 2020; Tian et al. 2023; Yan et al. 2024; Hévin and Condamine 2024), were selected as outgroups. In order to strengthen the backbone of the phylogeny, available sequences for five additional gene regions (ND5, ND1, 16S, EF1a and wg) were retrieved from GenBank and incorporated into our dataset (Table 1). Our dataset did not include nuclear sequences (EF1-a, wg) for south and central Anatolian populations. Alignment of sequences was done using MUSCLE modules implemented in AliView 1.28 (Larsson 2014) and double-checked visually. The final length of our dataset was 5865 basepairs. A maximum likelihood tree was obtained using IQTree web server (Nguyen et al. 2015). Bayesian analysis was conducted both in MrBayes 3.2.6 (Ronquist et al. 2012) as well as in BEAST (Suchard et al. 2018), each for 20 million generations. To calibrate the BEAST tree, we used estimates by Hévin and Condamine (2024) who present two sets of time-calibrated phylogenies for Parnassiinae with and without fossils. The differences in divergence time estimates between the two phylogenies are non-negligible, e.g. for the first split in the MRCA of *Archon* they infer 5.43 and 3.78 MYA (millions of years ago) respectively. We therefore used an average of the two dates estimated by these authors for three nodes relevant to this study under normal distribution and a sigma of 1: MRCA of *Archon*: 4.6 MYA, MRCA of *A. apollinaris* + *A. bostanchii*: 3.28 MYA, and MRCA of *A. apollinus* 1 + *A. apollinus* 2: 2.6 MYA. BEAST results were tested using TRACER 1.7.1 (Rambaut et al. 2018) and the consensus tree generated using TreeAnnotator v2.7.3 (Heled and Bouckaert 2013) with a burnin of 20%. Genetic distances were calculated using MEGA 11.0.8 (Tamura et al. 2021) under Kimura-2 parameter model.

Table 1. Material examined and GenBank accessions.

	SampleID	Species_name	Locality	Coordinates	COI	ND5	ND1	16S	EF1a	wg
1	not given	*Luehdorfia chinensis*			NC_027672	NC_027672	NC_027672	–	–	–
2	not given	*Luehdorfia japonica*			LT999996	LT999996	LT999996	AB186171	EF485102	DQ351138
3	not given	*Luehdorfia longicaudata*			NC_023938	NC_023938	NC_023938	–	DQ351114	–
4	not given	*Luehdorfia puziloi*			NC_072554	NC_072554	NC_072554	AB186170	DQ351115	DQ351139
5	W274	*Archon bostanchii*	Iran: Lorestan, Pol-e-Dokhtar	33.1478, 47.6957	AM284166	–	AM284158	AM284150	–	–
6	FS-b-2063	*Archon bostanchii*	Iran: Lorestan, Pol-e-Dokhtar	33.1478, 47.6957	DQ351033	DQ351052	DQ351070	DQ351096	DQ351113	DQ351137
7	G0823	*Archon bostanchii*	Iran: Khuzestan, N Andimeshk	32.4618, 48.3521	PV252017	–	–	–	–	–
8	G0824	*Archon bostanchii*	Iran: Khuzestan, N Andimeshk	32.4618, 48.3521	PV252041	–	–	–	–	–
9	G0825	*Archon bostanchii*	Iran: Khuzestan, N Andimeshk	32.4618, 48.3521	PV252045	–	–	–	–	–
10	MvS2025-G0740	*Archon bostanchii*	Iran: Khuzestan, N Andimeshk	32.4618, 48.3521	PV634285	–	–	–	–	–
11	MvS2025-G0742	*Archon bostanchii*	Iran: Khuzestan, N Andimeshk	32.4618, 48.3521	PV634288	–	–	–	–	–
12	W279	*Archon apollinaris*	Iran: Kermanshah	34.4719, 45.9751	AM231508	–	AJ972133	AJ972036	–	–
13	FS-b-2025	*Archon apollinaris*	Iran: Kermanshah, Rijab	34.4719, 45.9751	DQ351032	DQ351051	DQ351069	DQ351095	DQ351112	DQ351136
14	MvS2025-G0661	*Archon apollinaris*	Iran: Lorestan, Dorud	33.4973, 49.0355	PV634296	–	–	–	–	–
15	FS-b-2060	*Archon apollinaris*	Turkey: 33 km Mardin-Diayarbakir	37.56, 40.5395	DQ383991	–	–	–	–	–
16	W312	*Archon apollinaris*	Turkey: Diyarbakir, Ergani	38.2672, 39.7393	AM284164	–	AM284156	AM284148	–	–
17	G0598	*Archon apollinaris*	Turkey: env. Mardin	37.313, 40.734	PV252032	–	–	–	–	–
18	G0599	*Archon apollinaris*	Turkey: env. Mardin	37.313, 40.734	PV252021	–	–	–	–	–
19	W270	*Archon apollinaris*	Turkey: Mardin	37.313, 40.734	AM284165	–	AM284157	AM284149	–	–
20	MvS2025-G0576	*Archon apollinaris*	Turkey: Mardin	37.313, 40.734	PV634292	–	–	–	–	–
21	MvS2025-G0600	*Archon apollinaris*	Turkey: Mardin	37.313, 40.734	PV634289	–	–	–	–	–
22	MvS2025-G0602	*Archon apollinaris*	Turkey: Mardin	37.313, 40.734	PV634291	–	–	–	–	–
23	G0858	*Archon apollinaris*	Turkey: Tunceli, Ovacik	39.357, 39.2166	PV252046	–	–	–	–	–
24	G0866	*Archon apollinaris*	Turkey: Tunceli, Ovacik	39.357, 39.2166	PV252035	–	–	–	–	–
25	G0859	*Archon* sp.	Turkey: Tunceli, Ovacik	39.357, 39.2166	PV252026	–	–	–	–	–
26	G0867	*Archon* sp.	Turkey: Tunceli, Ovacik	39.357, 39.2166	PV252028	–	–	–	–	–
27	RVcoll.14-J599	*Archon apollinus*	Greece: Agiasos	39.07, 26.37	MW501103	–	–	–	–	–
28	MvS2025-G0486	*Archon apollinus*	Greece: Evros, Alexandroupoli	40.84, 25.87	PV634294	–	–	–	–	–
29	RVcoll.14-N558	*Archon apollinus*	Greece: Evros, Alexandroupoli	40.84, 25.87	MW500609	–	–	–	–	–
30	RVcoll.14-N559	*Archon apollinus*	Greece: Evros, Alexandroupoli	40.84, 25.87	MW501304	–	–	–	–	–
31	RVcoll.14-N560	*Archon apollinus*	Greece: Evros, Alexandroupoli	40.84, 25.87	MW502815	–	–	–	–	–
32	RVcoll.08-R594	*Archon apollinus*	Greece: Pirgos	37.71, 26.8	MW500195	–	–	–	–	–
33	RVcoll.09-X199	*Archon apollinus*	Greece: Pirgos	37.71, 26.8	MW500500	–	–	–	–	–
34	FS-b-2124	*Archon apollinus*	Greece: Samos	37.7245, 26.6528	DQ875936	–	–	–	–	–
35	2124	*Archon apollinus*	Greece: Samos	37.7245, 26.6528	LT999971	LT999971	–	–	–	–
36	G0797	*Archon apollinus*	Greece: Samos, W Koumaradei	37.75, 26.8333	PV252044	–	–	–	–	–
37	G0798	*Archon apollinus*	Greece: Samos, W Koumaradei	37.75, 26.8333	PV252012	–	–	–	–	–
38	W3	*Archon apollinus*	Turkey (locality not given)	-	AM231507	–	AJ972132	AJ972035	–	–
39	G0803	*Archon apollinus*	Turkey: Antalya, 10 km N Elmali	36.7305, 29.8815	PV252036	–	–	–	–	–
40	G0804	*Archon apollinus*	Turkey: Antalya, 10 km N Elmali	36.7305, 29.8815	PV252011	–	–	–	–	–
41	FS-b-2059	*Archon apollinus*	Turkey: Bursa, Yaliciftilic	40.3547, 28.7117	DQ383990	–	–	–	–	–
42	G0806	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252029	–	–	–	–	–
43	G0807	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252019	–	–	–	–	–

	SampleID	Species_name	Locality	Coordinates	COI	ND5	ND1	16S	EF1a	wg
44	G0808	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252038	–	–	–	–	–
45	G0809	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252027	–	–	–	–	–
46	G0810	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252030	–	–	–	–	–
47	G0811	*Archon apollinus*	Turkey: Canakkale, W Ezine	40.1467, 26.4086	PV252016	–	–	–	–	–
48	W332	*Archon apollinus*	Turkey: Efes	37.9355, 27.3435	AM284159	–	AM284151	AM284143	–	–
49	Omoto_etal_2004	*Archon apollinus*	Turkey: Izmir	38.4223, 27.14681	–	AB095661	AB186202	AB186168	–	–
50	MvS2025-G0642	*Archon apollinus*	Turkey: Mugla, Akbük	37.3878, 27.433	PV634297	–	–	–	–	–
51	G0800	*Archon apollinus*	Turkey: Mugla, Akbük	37.3878, 27.433	PV252006	–	–	–	–	–
52	G0801	*Archon apollinus*	Turkey: Mugla, Akbük	37.3878, 27.433	PV252004	–	–	–	–	–
53	FS-b-1868	*Archon apollinus*	Turkey: Mugla, Ölüdinez	36.5493, 29.1047	DQ351031	–	–	–	DQ351111	DQ351135
54	MvS2025-G0575	*Archon b. amasina*	Turkey: Amasya	40.6565, 35.8373	PV634293	–	–	–	–	–
55	W305	*Archon b. amasina*	Turkey: Ankara, Golbasi	39.7854, 32.7637	AM284161	–	AM284153	AM284145	–	–
56	W316	*Archon b. amasina*	Turkey: Diyarbakir	37.9228, 40.0803	AM284162	–	AM284154	AM284146	–	–
57	VNLEP00239	*Archon b. amasina*	Turkey: Erzurum, N Golyurt Gecidi, Akbulut	40.344, 40.822	PV252037	–	–	–	–	–
58	VNLEP00240	*Archon b. amasina*	Turkey: Erzurum, N Golyurt Gecidi, Akbulut	40.344, 40.822	PV252042	–	–	–	–	–
59	VNLEP00241	*Archon b. amasina*	Turkey: Erzurum, N Golyurt Gecidi, Akbulut	40.344, 40.822	PV252040	–	–	–	–	–
60	W260	*Archon b. amasina*	Turkey: Isparta, Isparta	37.7901, 30.5086	AM284160	–	AM284152	AM284144	–	–
61	G0818	*Archon b. amasina*	Turkey: N Amasya	40.6565, 35.8373	PV252033	–	–	–	–	–
62	G0819	*Archon b. amasina*	Turkey: N Amasya	40.6565, 35.8373	PV252039	–	–	–	–	–
63	MvS2025-G0651	*Archon b. amasina*	Turkey: Nevshehir	38.6328, 34.6675	PV634286	–	–	–	–	–
64	CCDB-23377 A01	*Archon b. bellargus*	occupied territories/ West Bank	31.0461, 34.8491251	PV252025	–	–	–	–	–
65	CCDB-23377 A02	*Archon b. bellargus*	occupied territories/ West Bank	31.0461, 34.8491251	PV252022	–	–	–	–	–
66	CCDB-23377 A03	*Archon b. bellargus*	occupied territories/ West Bank	31.0461, 34.8491251	PV252018	–	–	–	–	–
67	G0812	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252010	–	–	–	–	–
68	G0814	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252003	–	–	–	–	–
69	G0816	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252031	–	–	–	–	–
70	G0820	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252008	–	–	–	–	–
71	G0821	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252007	–	–	–	–	–
72	G0822	*Archon b. bellargus*	Israel: 15 km W Jerusalem	31.731942, 35.036116	PV252009	–	–	–	–	–
73	CCDB-17967 E02	*Archon b. bellargus*	occupied territories/ West Bank	33.089, 35.4669	PV252043	–	–	–	–	–
74	MCZ:HU-08-A007	*Archon b. bellargus*	Israel: Ben-Shemen Forest	31.947, 34.9482	PV252015	–	–	–	OK737458	OK747464
75	MvS2025-G0377	*Archon b. bellargus*	Israel: Ben-Shemen Forest	31.947, 34.9482	PV634295	–	–	–	–	–
76	MvS2025-G0786	*Archon b. bellargus*	Israel: Bet Shemesh	31.7277, 34.9484	PV634290	–	–	–	–	–
77	MvS2025-G0787	*Archon b. bellargus*	Israel: Bet Shemesh	31.7277, 34.9484	PV634287	–	–	–	–	–
78	FS-b-2024	*Archon b. bellargus*	occupied territories/ West Bank	31.8478, 34.9828	DQ383989	–	–	–	–	–
79	CCDB-17967 A11	*Archon b. bellargus*	Israel: Jerusalem	31.781, 35.2066	PV252014	–	–	–	–	–
80	CCDB-17967 A12	*Archon b. bellargus*	Israel: Jerusalem	31.781, 35.2066	PV252023	–	–	–	–	–
81	BC ZSM Lep 56961	*Archon b. bellargus*	Israel: Jerusalem Mts, NE Ein Kerem	31.7667, 35.15	PV277995	–	–	–	–	–
82	MvS2025-G0788	*Archon b. bellargus*	Syria: Merom Golan	33.133, 35.7712	PV634298	–	–	–	–	–
83	G0826	*Archon b. bellargus*	Lebanon: Faitroun, NE Beirut	33.9922, 35.7374	PV252047	–	–	–	–	–
84	G0827	*Archon b. bellargus*	Lebanon: Faitroun, NE Beirut	33.9922, 35.7374	PV252034	–	–	–	–	–

	SampleID	Species_name	Locality	Coordinates	COI	ND5	ND1	16S	EF1a	wg
85	G0828	*Archon b. bellargus*	Lebanon: Faitroun, NE Beirut	33.9922, 35.7374	PV252005	–	–	–	–	–
86	G0836	*Archon b. bellargus*	Turkey: Hatay, 9 km S Harbiye, vic. Yukari-ocela	36.0881, 36.1468	PV252024	–	–	–	–	–
87	G0837	*Archon b. bellargus*	Turkey: Hatay, 9 km S Harbiye, vic. Yukari-ocela	36.0881, 36.1468	PV252013	–	–	–	–	–
88	G0844	*Archon b. bellargus*	Turkey: Hatay, S Antakya region, Senköy	36.0488, 36.1437	PV252020	–	–	–	–	–
89	G0845	*Archon b. bellargus*	Turkey: Hatay, S Antakya region, Senköy	36.0488, 36.1437	PV252002	–	–	–	–	–
90	W308	*Archon b. bellargus*	Turkey: Hatay, S. Antakya	36.221, 36.0832	AM284163	–	AM284155	AM284147	–	–

Results

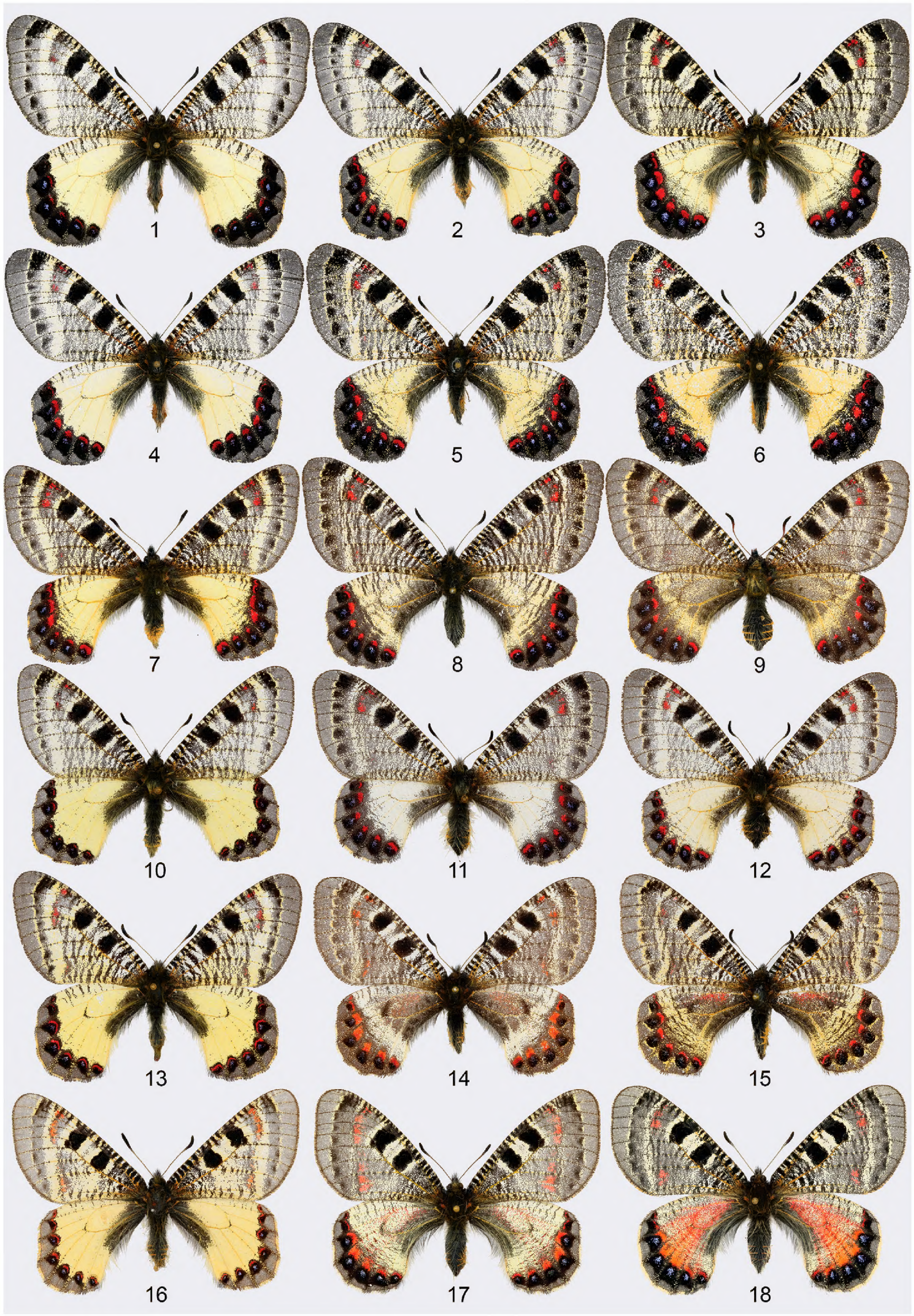
A summary of variable characters is presented in Table 2.

Adult morphology (Figs 1–18). Adults of *A. apollinus* from the Levant show large, deep black submarginal spots on the hind wings, which are also very pronounced on the underside and almost always have an intense blue colouring on the upper side. The red lunulae of the hind wings are bright dark red and always clearly outlined. Also typical for individuals from the Levant is a marbling pattern of the submarginal band that runs across the veins of the hind wings, while the proximal extent and intensity varies from individual to individual (Figs 1–15). In contrast, in western Turkish adults the black submarginal spots are less developed and the submarginal banding of the hind wings barely extends beyond the red lunulae. In addition, the red spots are not so clearly outlined and often merge with a red suffusion of the hindwings in the females that sometimes extends as far as the wing base. Occasionally, impressive individuals with intensely red suffused hind wings occur. A proximal black marbling of the hind wings is hardly pronounced (Figs 16–18).

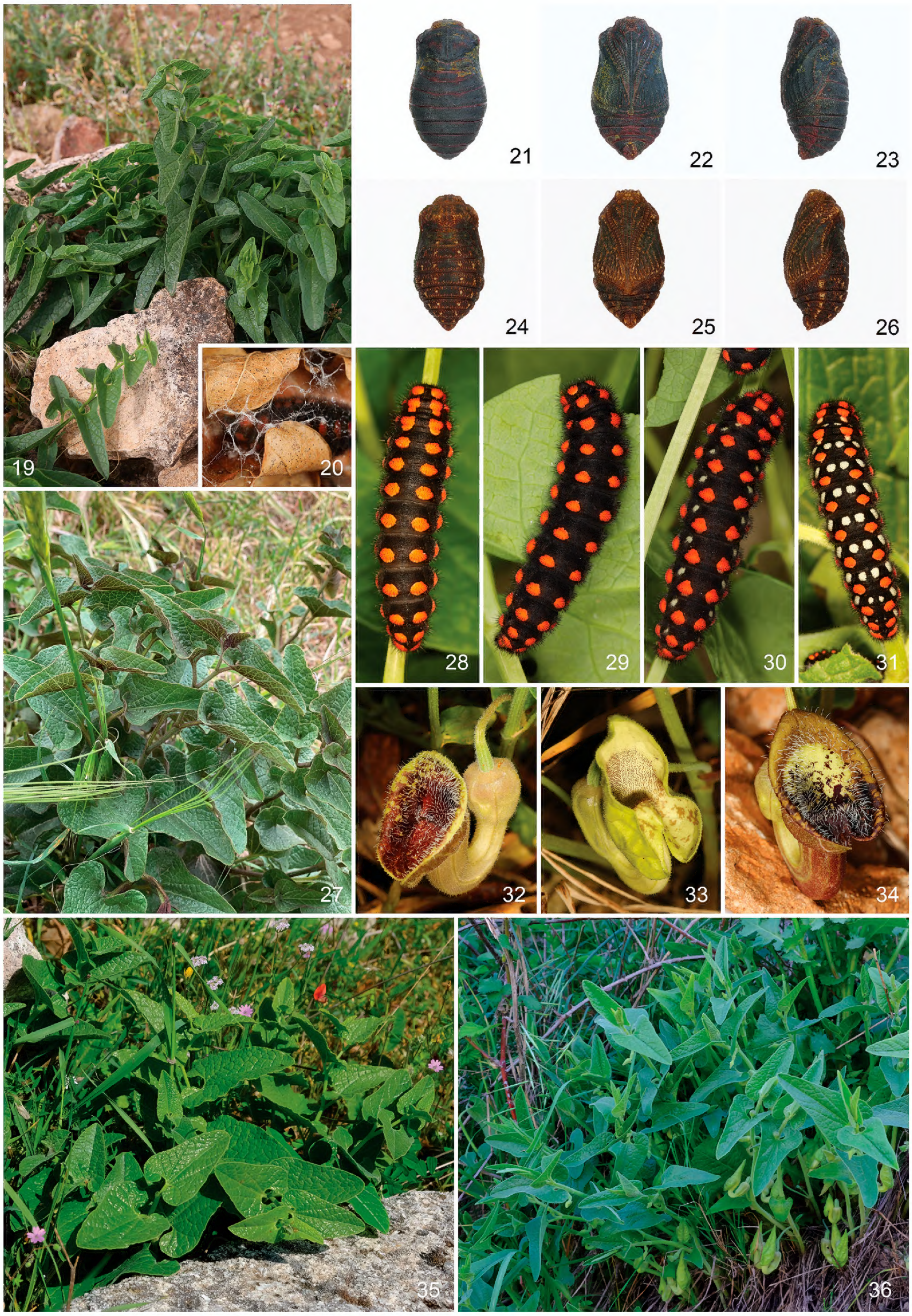
Larval host plants (Figs 19–36). Throughout the species range, *A. apollinus* larvae feed on many different herbaceous species of *Aristolochia*. In western Turkey the main hosts are species in the *Aristolochia hirta* L. complex, (including *Aristolochia bodamae* Dingler, Figs 32, 35) and in central-eastern Turkey, *Aristolochia bottae* Jaub. & Spach (Fig. 19) and *Aristolochia maurorum* L. The latter occurs as far south as the southern Turkish province of Hatay, and is replaced by *Aristolochia paecilantha* Boiss (Figs 27, 33, 36) in the Levant. In southern Levant, the primary hosts are *Aristolochia bottae* and *Aristolochia paecilantha*. While *A. bottae* (Fig. 34) belongs to the Irano-Turanian floral elements and occurs here in a geno- and phenotypic variant compared to eastern Turkey and Iran (Mahfoud 2010), *A. paecilantha* is found exclusively in the Levant. In Israel *Archon apollinus* normally flies between March and April, but unlike in Anatolia, depending on altitude and weather conditions it can be seen even in November and December. Because *Aristolochia paecilantha* and *Aristolochia bottae* have not yet sprouted in early winter, adults hatching so early in the year alternatively use *Aristolochia parvifolia* Sm. as a depository and larval hostplant. The butterflies are very site-dependent and can always be found close to the larval hostplants. They lay their eggs early on the newly-sprouting stems in small batches close to the ground. Hatching caterpillars migrate to the shoot pole and live there hidden in the tender, still folded apical leaves. Only later do they switch to mature, older and lower lying leaves. The caterpillars spin the leaves together with silk to form protective bags (Fig. 20). This behaviour, which is seen across the range of *Archon*, offers a certain degree of protection from parasitoids, especially from ichneumonid wasps.

Larval morphology (Figs 28–31). Among the caterpillars whose photos were examined, those from the Levant (n = 127) and Antakya (n = 123), with very few exceptions, showed a consistently unique appearance with a velvety black background and four longitudinal rows of strong orange-red spots (Fig. 28, 29). Among these, only four individuals (1%) had additional rows of smaller white spots (Fig. 30). In contrast, all caterpillars examined from Western (n = 78) and Central Turkey (n = 12) had large supplementary rows of white or greenish-white spots (Fig. 31).

Pupal morphology (Figs 21–26). The difference between western Turkish/Greek and Levantine populations is even clearer in the pupae (Figs 21–26). The hardened pupae from the Levant (Figs 24–26) are of a fawn-brown basic colour throughout and have a light longitudinal dot pattern ventrally. Dorsally, the wing-vein reliefs are lighter brown contrasting with the darker ground colour, and the abdominal end is more pointed than in western Turkish populations. The western Turkish pupae are easily and clearly recognisable by their uniform, black-reddish ground colour and show neither a ventral dot pattern nor a dorsal colour-contrasting wing vein (Figs 21–23). All *Archon* caterpillars (*A. apollinus* and *A. bellargus*) in Turkey and the Levant spin leaves to create protective bags during their life; however, shortly before pupation, the Levantine caterpillars produce a loose webbing (Fig. 20), which does not seem to be the case with caterpillars in western Turkey.



Figures 1–18. Representatives of genus *Archon* examined in this study. **1–6**. *A. bellargus* (Staudinger, [1892]), Israel, Bet Shemesh, 300 m, 30.III.1987; **7–9**. *A. bellargus "drusica"* (De Freina & Leestmans, 2003), Syria, Djebel el Druz, 1250 m, 10.-11.IV.1988, leg. de Freina; **7.** Holotype; **8, 9.** Paratype; **10, 12**. *A. bellargus*, Lebanon, Sofar, E Beirut, 1300 m, 7.-16.IV.1968, leg. Rose; **11**. *A. bellargus*, Lebanon, Feitroun, NE Beirut, 1200 m, 04.-15.IV.1968, leg. Rose; **13–15**. *A. bellargus*, SE Turkey, Prov. Hatay, S Antakya, 4.-12.IV.1988, leg. J. Cl. Weiss; **16**. *A. apollinus* (Herbst, 1789), Neotype, Turkey, Izmir, March 1969, leg. Rubyk; **17**. *A. apollinus*, SW Turkey, Ephesus, 60 m, e.l., 3.III.1973; **18**. *A. apollinus* (Herbst, 1789), NW-Turkey, Çanakkale, 50 m, e.l., 6.III.1973.



Figures 19–36. Larval host plants and the early stages of species of *Archon*. **19**. *Aristolochia bottae*, Turkey, Mardin; **20**. caterpillar of *Archon bellargus* spinning a web, Turkey, Hatay, Antakya; **21–23**. Pupae of *Archon apollinus*, Turkey, Çanakkale; **24–26**. Pupae *A. bellargus*, Israel, Bet Shemesh; **27**. *Aristolochia paecilantha*, Israel, Bet Shemesh; **28**. Caterpillar of *Archon bellargus*, Israel, Bet Shemesh; **29**. caterpillar of *Archon bellargus*, Turkey, Hatay, Antakya; **30.** Caterpillar of *Archon bellargus*, Turkey, Hatay, Antakya; pattern variety less than 1% of the examined caterpillars; **31.** Caterpillar of *Archon apollinus*, Turkey, Alexandria Troas; **32**. *Aristolochia bodamae* flower, Turkey, Çanakkale; **33**. *Aristolochia paecilantha* flower, Turkey, Antakya; **34**. *Aristolochia bottae* flower, Turkey, Mardin; **35**. *Aristolochia bodamae*, Turkey, Çanakkale; **36**. *Aristolochia paecilantha*, Turkey, Antakya.

Genitalia (Figs 37–47). In male genitalia of samples from Greece, Western and Central Turkey (Figs 37–39), the tip of the uncus is curved, the vinculum is short, and the phallus is proportionally shorter. In contrast, in samples from Antakya and Israel (Figs 40, 41), the tip of the uncus is straight, and the vinculum and the phallus are proportionally longer. These configurations are different and the genitalia are proportionally smaller in sister species *A. apollinaris* and *A. bostanchii* (Figs 42–43). The female genitalia in *A. apollinus* (Fig. 44) and *A. bellargus* (Fig. 45) also show a number of distinct differences in the shape and extent of the sclerotized parts of abdominal segment 8 and corpus bursae, and these are, in turn, also different from *A. apollinaris* and *A. bostanchii* (Figs 46, 47).

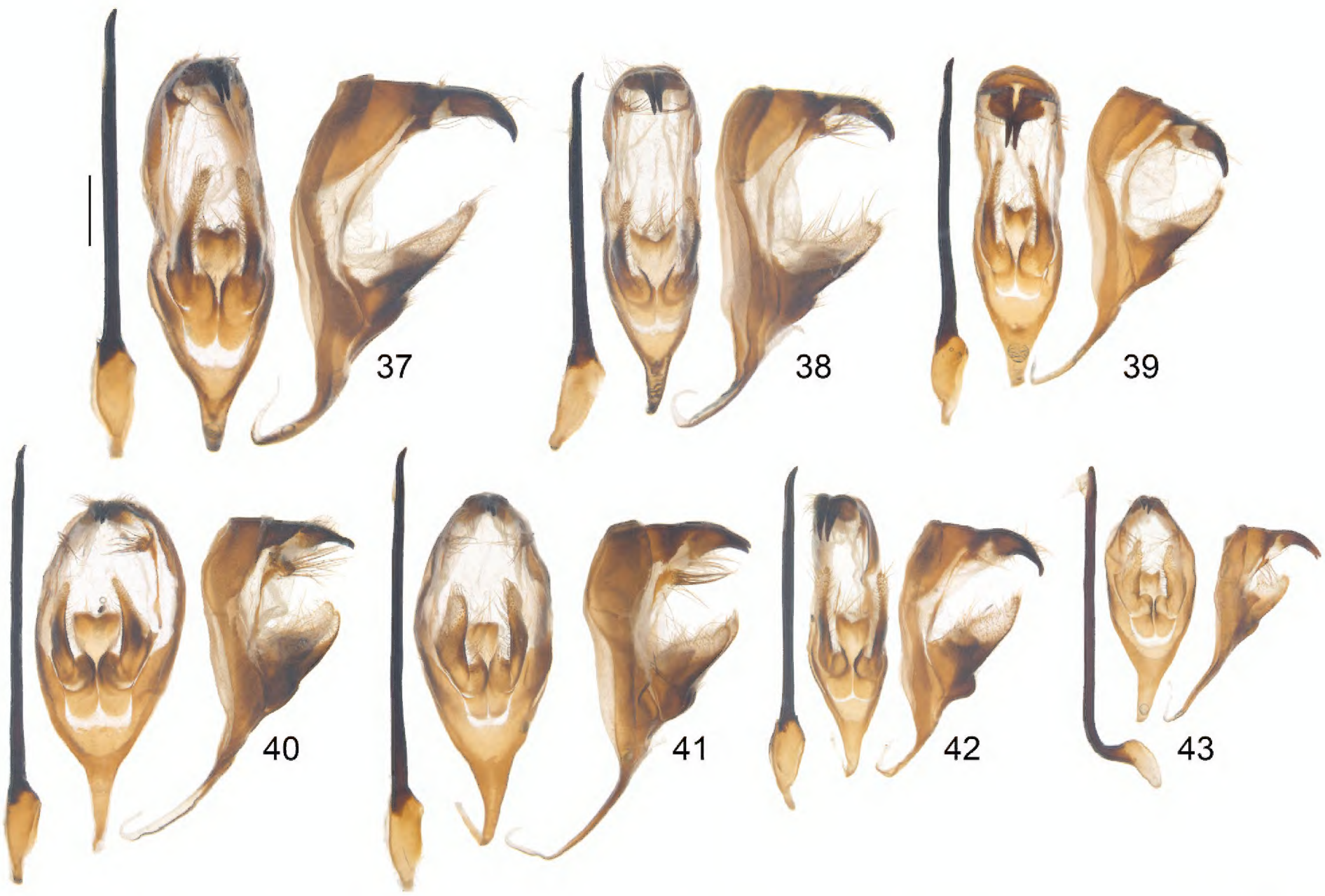
Molecular data (Figs 48, 49). Genetic distances for COI-barcodes calculated under Kimura-2 parameter (Table 3) show lower values compared to the results reported by Nazari and Sperling (2007), however it should be noted that the latter authors used a longer, non-overlapping fragment of COI closer to the 3' end of this gene region. Our inferred ages for the split events in the MRCA of *A. apollinaris* + *A. bostanchii* (3.16 MYA) and that of *A. apollinus* + *A. bellargus* (2.86 MYA) suggest a shared geological age in Pliocene, and by extension, a comparable taxonomic rank (separate species) for these taxa.

Our larger sampling of *A. apollinus* populations throughout the species' range confirms the deep divergence between the Western Turkish and the Levantine populations, but also clarifies the ranges of these genotypes. The two well-supported clades within *A. apollinus* include: A) populations from western Turkey (type locality) and Greece, ranging from Alexandroupoli (Evros) and the Aegean Islands to Antalya, and B) populations from central and southern Anatolia to the Levant. The populations from central Anatolia (ssp. *amasina*) appear as a minimally-differentiated sub-lineage within the second clade (Fig. 49). Finally, two of our samples *A. apollinaris* from Ovaçik, Tunceli (G0859 and G0867) produced high quality COI barcode sequences that matched those of *A. apollinus*.

Discussion

Levantine *Archon bellargus* as a separate species

The Levantine *Archon* is phenotypically distinct from all Turkish and Greek populations. Adults show differences in genitalia and wing markings and, unlike the Turkish and Greek populations, fly partially in early winter.



Figures 37–43. Male genitalia of *Archon* showing (from left to right) the phallus, ventral-, and lateral aspects of the genitalia; **37.** *A. apollinus*, Turkey: Alexandria Troas, diss. 1267; **38.** *A. apollinus*, Turkey: Mugla, diss. 1266; **39.** *A. bellargus amasina*, Turkey: Amasya, diss. 1272; **40.** *A. bellargus bellargus*, Turkey: Antakya, diss. 1270; **41.** *A. bellargus bellargus*, Israel: Bet Shemesh, diss. 1269; **42.** *A. apollinaris*, Iran: Lorestan, diss. 1275; **43.** *A. bostanchii*, Iran: Khuzestan, diss. 1274. Scale bar: 1 mm.

Table 2. Summary of characters that show variation in *Archon apollinus* and *Archon bellargus* stat. nov.

Character	*Archon apollinus*	*Archon bellargus* ssp. *bellargus*	*Archon bellargus* ssp. *amasina*
Distribution	Greece, W. Turkey	Hatay to Israel	central Turkey
Adult morphology	HW submarginal spots less developed, submarginal banding barely extends beyond the red lunulae, black cellular spot rarely developed	HW submarginal spots large, deep black with intense blue coloring, submarginal band runs across HW veins, black cellular spot rarely developed	HW submarginal spots less developed, submarginal banding barely extends beyond the red lunulae, black cellular spot almost always developed
Male genitalia	tip of the uncus curved, vinculum proportionally shorter	tip of the uncus straight, vinculum proportionally longer	tip of the uncus curved, vinculum proportionally shorter
Hostplants	*A. bodame*, *A. hirta*, *A. auricularia*, *A. baseri*, *A. guichardii*, *A. incisa*	*A. bottae*, *A. maurorum*, *A. paecilantha*, *A. parvifolia* (secondary)	*A. bottae*, *A. maurorum*
Flight period	March-April	February-April, Nov-Dec	March-early April
Larval morphology	lighter spots usually present	velvety black with four longitudinal rows of orange-red spots; lighter spots usually absent	lighter spots usually present
Pupal morphology	uniform reddish-black without ventral dot pattern; wing vein-relief same color as pupa; abdominal end less pointed	fawn-brown with light longitudinal dot pattern ventrally; wing vein relief lighter brown; abdominal end more pointed	uniform reddish-black without ventral dot pattern; wing vein-relief same color as pupa; abdominal end less pointed

Table 3. Kimura 2-parameter (K2P) distances in COI barcodes among specimens of *Archon* examined in this study.

	A. apollinaris	*A. bostanchii*	*A. apollinus*	*A. bellargus amasina*	*A. bellargs bellargs*
(n = 12)	0.71 ± 0.46				
(n = 7)	2.24 ± 0.36	0.38 ± 0.32			
(n = 24)	2.75 ± 0.4	1.86 ± 0.23	0.34 ± 0.24		
(n = 10)	2.5 ± 0.32	1.73 ± 0.2	**1.47 ± 0.24**	0.24 ± 0.2	
(n = 27)	2.46 ± 0.36	1.47 ± 0.23	**1.23 ± 0.21**	0.45 ± 0.2	0.21 ± 0.21

Figures 44–47. Female genitalia of *Archon* showing (from left to right) the lateral and ventral aspects. **44.** *A. apollinus*, Turkey: Alexandria Troas, diss. 1268; **45.** *A. bellargus*, Israel: Bet Shemesh, diss. 1271; **46.** *A. apollinaris*, Iran: Lorestan, diss. 1276; **47.** *A. bostanchii*, Iran: Khuzestan, diss. 1274. Scale bar: 1 mm.

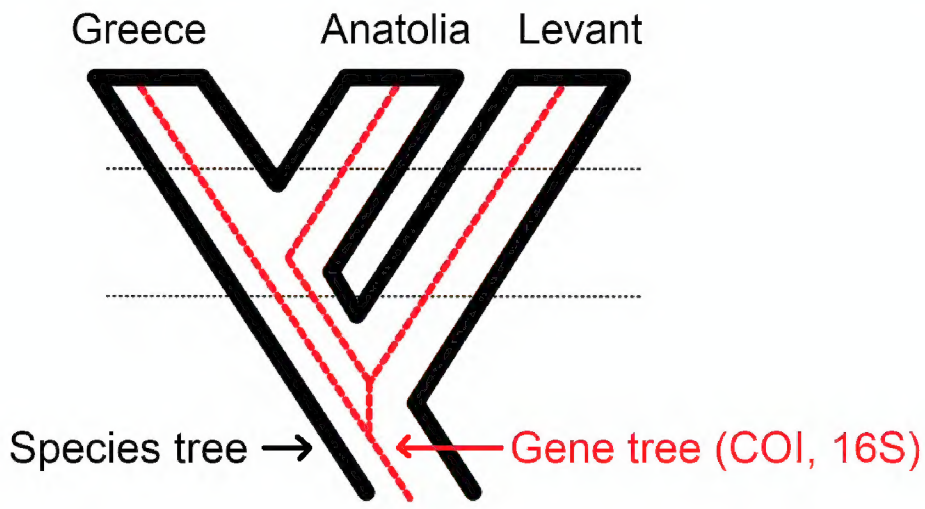


Figure. 48. Gene tree vs. Species tree discordance in *Archon*.

The caterpillars are phenotypically different and feed on different species of *Aristolochia*, and before pupation they spin a peculiar web that appears to be unique to these populations. Their pupae are also different in shape and color. These differences support their distinct status. Our genetic data suggests that the Hatay populations (type locality of the taxon *bellargus* Staudinger [1892]) are closely related to Levantine group. Since this is the oldest available name for these populations, thus we recognize this name as the valid name to be used for the new species, *Archon bellargus* (Staudinger, [1892]), stat. nov.

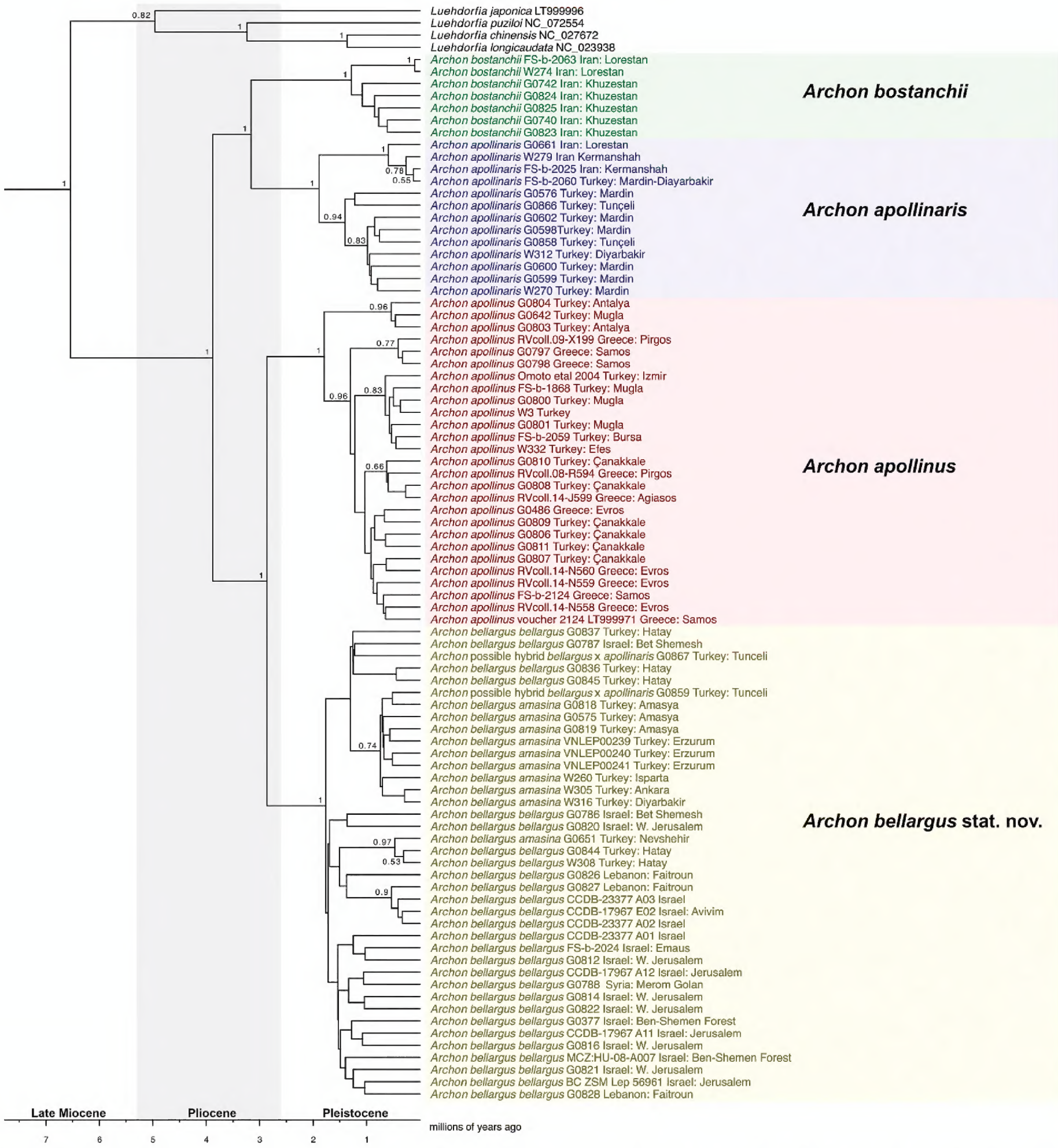

Luehdorfia japonica LT999996
Luehdorfia puziloi NC_072554
Luehdorfia chinensis NC_027672
Luehdorfia longicaudata NC_023938
Archon bostanchii FS-b-2063 Iran: Lorestan
Archon bostanchii W274 Iran: Lorestan
Archon bostanchii G0742 Iran: Khuzestan
Archon bostanchii G0824 Iran: Khuzestan
Archon bostanchii G0825 Iran: Khuzestan
Archon bostanchii G0740 Iran: Khuzestan
Archon bostanchii G0823 Iran: Khuzestan
Archon bostanchii
Archon apollinaris G0661 Iran: Lorestan
Archon apollinaris W279 Iran Kermanshah
Archon apollinaris FS-b-2025 Iran: Kermanshah
Archon apollinaris FS-b-2060 Turkey: Mardin-Diayarbakir
Archon apollinaris G0576 Turkey: Mardin
Archon apollinaris G0866 Turkey: Tunçeli
Archon apollinaris G0602 Turkey: Mardin
Archon apollinaris G0598Turkey: Mardin
Archon apollinaris G0858 Turkey: Tunçeli
Archon apollinaris W312 Turkey: Diyarbakir
Archon apollinaris G0600 Turkey: Mardin
Archon apollinaris G0599 Turkey: Mardin
Archon apollinaris W270 Turkey: Mardin
Archon apollinaris
Archon apollinus G0804 Turkey: Antalya
Archon apollinus G0642 Turkey: Mugla
Archon apollinus G0803 Turkey: Antalya
Archon apollinus RVcoll.09-X199 Greece: Pirgos
Archon apollinus G0797 Greece: Samos
Archon apollinus G0798 Greece: Samos
Archon apollinus Omoto etal 2004 Turkey: Izmir
Archon apollinus FS-b-1868 Turkey: Mugla
Archon apollinus G0800 Turkey: Mugla
Archon apollinus W3 Turkey
Archon apollinus G0801 Turkey: Mugla
Archon apollinus FS-b-2059 Turkey: Bursa
Archon apollinus W332 Turkey: Efes
Archon apollinus G0810 Turkey: Çanakkale
Archon apollinus RVcoll.08-R594 Greece: Pirgos
Archon apollinus G0808 Turkey: Çanakkale
Archon apollinus RVcoll.14-J599 Greece: Agiasos
Archon apollinus G0486 Greece: Evros
Archon apollinus G0809 Turkey: Çanakkale
Archon apollinus G0806 Turkey: Çanakkale
Archon apollinus G0811 Turkey: Çanakkale
Archon apollinus G0807 Turkey: Çanakkale
Archon apollinus RVcoll.14-N560 Greece: Evros
Archon apollinus RVcoll.14-N559 Greece: Evros
Archon apollinus FS-b-2124 Greece: Samos
Archon apollinus RVcoll.14-N558 Greece: Evros
Archon apollinus voucher 2124 LT999971 Greece: Samos
Archon apollinus
Archon bellargus bellargus G0837 Turkey: Hatay
Archon bellargus bellargus G0787 Israel: Bet Shemesh
Archon possible hybrid bellargus x apollinaris G0867 Turkey: Tunceli
Archon bellargus bellargus G0836 Turkey: Hatay
Archon bellargus bellargus G0845 Turkey: Hatay
Archon possible hybrid bellargus x apollinaris G0859 Turkey: Tunceli
Archon bellargus amasina G0818 Turkey: Amasya
Archon bellargus amasina G0575 Turkey: Amasya
Archon bellargus amasina G0819 Turkey: Amasya
Archon bellargus amasina VNLEP00239 Turkey: Erzurum
Archon bellargus amasina VNLEP00240 Turkey: Erzurum
Archon bellargus amasina VNLEP00241 Turkey: Erzurum
Archon bellargus amasina W260 Turkey: Isparta
Archon bellargus amasina W305 Turkey: Ankara
Archon bellargus amasina W316 Turkey: Diyarbakir
Archon bellargus bellargus G0786 Israel: Bet Shemesh
Archon bellargus bellargus G0820 Israel: W. Jerusalem
Archon bellargus amasina G0651 Turkey: Nevshehir
Archon bellargus bellargus G0844 Turkey: Hatay
Archon bellargus bellargus W308 Turkey: Hatay
Archon bellargus bellargus G0826 Lebanon: Faitroun
Archon bellargus bellargus G0827 Lebanon: Faitroun
Archon bellargus bellargus CCDB-23377 A03 Israel
Archon bellargus bellargus CCDB-17967 E02 Israel: Avivim
Archon bellargus bellargus CCDB-23377 A02 Israel
Archon bellargus bellargus CCDB-23377 A01 Israel
Archon bellargus bellargus FS-b-2024 Israel: Emaus
Archon bellargus bellargus G0812 Israel: W. Jerusalem
Archon bellargus bellargus CCDB-17967 A12 Israel: Jerusalem
Archon bellargus bellargus G0788 Syria: Merom Golan
Archon bellargus bellargus G0814 Israel: W. Jerusalem
Archon bellargus bellargus G0822 Israel: W. Jerusalem
Archon bellargus bellargus G0377 Israel: Ben-Shemen Forest
Archon bellargus bellargus CCDB-17967 A11 Israel: Jerusalem
Archon bellargus bellargus G0816 Israel: W. Jerusalem
Archon bellargus bellargus MCZ:HU-08-A007 Israel: Ben-Shemen Forest
Archon bellargus bellargus G0821 Israel: W. Jerusalem
Archon bellargus bellargus BC ZSM Lep 56961 Israel: Jerusalem
Archon bellargus bellargus G0828 Lebanon: Faitroun
Archon bellargus stat. nov.
0.82
1
1
1
1
1
1
1
1
0.78
0.55
1
0.94
0.83
0.96
0.77
1
0.96
0.83
0.66
1
0.74
1
0.97
0.53
0.9
Late Miocene
Pliocene
Pleistocene
7
6
5
4
3
2
1
millions of years ago

Figure. 49. Bayesian phylogeny of the combined dataset of six gene regions for *Archon* and *Luehdorfia* outgroups. Posterior probabilities are shown only for supported nodes (<0.5%). Colors correspond to the dots on the distribution map in Fig. 37.

Incomplete lineage sorting between *A. apollinus* and *A. bellargus*

Genotypically, the Levantine populations show a strong affinity with those in south/central Anatolia. This is evident not only in COI barcodes, but also in ribosomal 16S gene, even though the latter is also part of the mitochondrial genome and forms a linkage group with COI (Fig. 48). In contrast, the south/central Anatolian populations are phenotypically closer to those in western Turkey and Greece: The morphology of the adults, larvae and pupae all resemble those of *A. apollinus*, and the pre-pupal larvae do not spin a web as in the Levantine populations. This is a classic case of discordance between gene trees and species trees: While the 'species tree' (in this case assumed based on traditional morphological and biological characters discussed above) suggests that the central Anatolian populations are part of the variation within the western Anatolian/Greek species *A. apollinus*, mitochondrial and ribosomal gene sequences instead suggest that these populations are part of the larger variation in the Levantine species *A. bellargus* (Fig. 49). Gene tree/species tree discordance (a.k.a. Incomplete Lineage Sorting) occurs either as a result of genetic introgression, or when at the time of speciation, the ancestral population is polymorphic (Maddison 1997). In such cases, examination of additional genetic data can shed light on the "true" phylogeny (Brower et al. 1996; Brower and Schuh 2021). For *Archon*, sequence data from two gene regions (mitochondrial COI and the linked ribosomal 16S) both show the same pattern, supporting the affinity of the central Anatolian populations with *A. bellargus*. However, since the populations with similar genetic composition are in geographical proximity, genetic introgression cannot be ruled out.

Our phylogenetic analysis suggests that the isolating event that separated the populations currently flying in Greece and Western Turkey from those in Central Anatolia and Levant occurred in the Miocene, around 9.5 million years ago, allowing for a deep genetic differentiation to accrue between these two groups over a long period of time. The sea level oscillations during this period that resulted in changing coastal plains and repeated connection and disconnection between the Mediterranean and Paratethys undoubtedly played some role in this vicariant event. Even though subsequent changes in geological topography of the region followed by dispersal, migration and extinctions likely changed the distributional landscape of these populations, the caterpillars of both eastern and western Anatolian groups continued to feed on the same host plants and enjoyed more humid climatic conditions than those in the Levant. A second isolating event that separated the Levantine populations from the genetic stock in Central Anatolia occurred much later in Pleistocene, probably as a result of drier climatic conditions, a shift in larval host plants, and possibly also the presence of parasitoids in the Levant. While these factors likely played a role in the altered morphology and ethology of this population, their genetic make-up remained close to the Central Anatolian group. To reconcile a taxonomic solution, for the time being we tentatively recognize the oldest available name for central Anatolian populations as a subspecies of the Levantine species, *A. bellargus amasina* Staudinger, 1901, stat. nov. (Fig. 50). Additional genetic data are required to confirm the status of these populations.

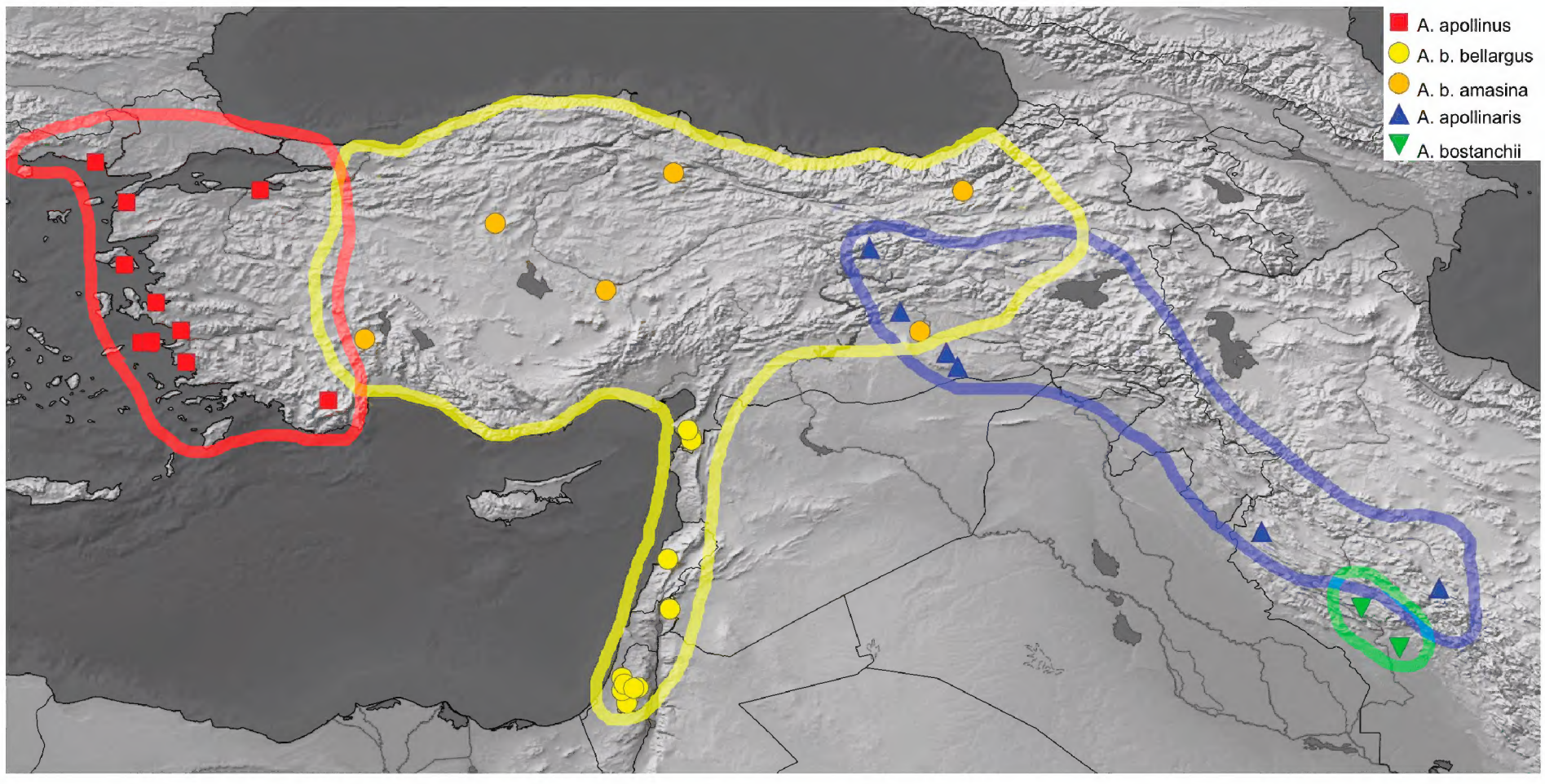


Figure 50. Distribution of barcoded specimens.

Hybridization between *A. bellargus* and *A. apollinaris*

Of the four samples of *A. apollinaris* barcoded in our study from Ovaçik, Tunceli (Turkey), two (G0858 and G0866) produced genuine *A. apollinaris* sequences, while the other two (G0859 and G0867) yielded high quality sequences that matched those of *A. bellargus amasina*. This area falls within a hypothetical boundary between the two species (Hesselbarth et al. 1995; Carbonell and Michel 2007). We posit that the *Archon* in Ovaçik, and perhaps others in the overlapping region, may be a hybrid population with polymorphic mtDNA resulting from secondary contact and interbreeding of *Archon bellargus* and *A. apollinaris*. Further research is needed to confirm the status of these populations.

Acknowledgements

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